

SKULL AND SWIMBLADDER CONNECTIONS IN FISHES OF THE FAMILY MEGALOPIDAE

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CONTENTS

	Page
INTRODUCTION	121
THE LINKAGE BETWEEN SKULL AND SWIMBLADDER IN <i>Megalops cyprinoides</i>	122
The soft tissues	122
Otic region of the skull	124
SKULL AND SWIMBLADDER LINKAGE IN <i>Tarpon atlanticus</i>	125
The soft tissues	125
Otic region of the skull	127
THE SACCULAR OTOLITH IN <i>Megalops</i> AND <i>Tarpon</i>	128
SWIMBLADDER-SKULL CONNECTIONS IN OTHER ELOPIFORM FISHES	130
DISCUSSION	131
The status of the genera <i>Megalops</i> and <i>Tarpon</i>	131
Relationships between the Elopomorpha and Clupeomorpha	132
SUMMARY	133
ACKNOWLEDGEMENTS	133
APPENDIX: Notes on the caudal fin skeleton in <i>Megalops</i> and <i>Tarpon</i>	133
REFERENCES	134
LIST OF ABBREVIATIONS USED IN THE FIGURES	135

INTRODUCTION

THE only detailed account of connections between the swimbladder and the otic region in megalopid fishes is that given by de Beaufort (1909), who described the Indo-Pacific Oxeye, *Megalops cyprinoides* (Brouss.). The closely related Atlantic species *Tarpon atlanticus* (C. and V.) is mentioned in de Beaufort's paper solely by the quotation of Hyrtl's (1855) brief description of the swimbladder. No comparative study, or comment, was made by de Beaufort.

Hyrtl's remarks are rather vague and would not lead one to suspect the existence of any marked interspecific differences in swimbladder anatomy. Later authors, as did de Beaufort, have tacitly assumed that the swimbladder and its otic connections are alike in both species.

Externally, the two species are very similar, and there is still a great deal of uncertainty about the generic status of the Atlantic Tarpon. Some authors treat it as a monotypic genus, *Tarpon atlanticus*, while others refer it to the genus *Megalops* (see Hollister, 1939, and Hildebrand, 1963, for further discussion). This problem will be considered anew in the light of the marked interspecific differences which I have found in many details of the skull-swimbladder linkage, and in the otic region of the skull.

Other taxonomic problems, but particularly the relationship between the Elopomorpha and the Clupeomorpha, will also be discussed (see Greenwood *et al.*, 1966).

THE LINKAGE BETWEEN SKULL AND SWIMBLADDER IN
MEGALOPS CYPRINOIDES

In general, my investigation of the swimbladder in this species confirms the description given by de Beaufort (1909). The situation is redescribed here in some detail mainly to serve as a basis for comparison with *Tarpon atlanticus* (see pp. 125-8).

The soft tissues. There is one aspect where de Beaufort and I differ, and that is in our interpretation of the outer thickened tunic which covers the precoelomic extension of the swimbladder.

The tunic is identified by de Beaufort as swimbladder wall which has become greatly thickened and differentiated into an anterior, transversely aligned, "U"-shaped portion linking the periotic bullae with the longer egg-shaped part running forward from the pneumatic duct (see de Beaufort, 1909, p. 529; fig. 2, and plate 29, fig. 3). de Beaufort does not identify precisely which of the swimbladder tunics is thickened, but his figures and description would seem to imply that it is the tunica externa. Certainly his figure 2 shows the egg-shaped portion as continuous with the outer wall of the main bladder. He is quite explicit in identifying the tissue which enters the periotic bullae (the "U"-shaped part remaining outside) as tunica interna.

I find, however, that the thickened tissue of the egg-shaped portion is actually continuous with the much thinner peritoneal membrane covering the ventral and lateral aspects of the main swimbladder. Although the thick and thin parts of the peritoneum are continuous, there is no obvious gradient in thickness between them. Instead, there is a clear-cut line of demarcation running obliquely upwards and posteriorly from a point just anterior to the pneumatic duct. Without special care in dissection, the peritoneum parts cleanly along this line. The thin tissue then collapses and adheres closely to the swimbladder, while the thick walled egg-shaped portion retains its shape. In this condition the egg-shaped part certainly does not appear to be part of the peritoneal lining, but nor does it seem to be part of the swimbladder, which can be seen lying within it.

From a careful dissection of the tissues involved, and considering that the egg-shaped portion is continuous with the peritoneum, I find it difficult to interpret the precoelomic, thick-walled tunic as being derived from intrinsic swimbladder tissue. Instead, I would interpret it as being derived from the peritoneum; in effect, an evagination of the transverse septum. Thus, the precoelomic portion of the swimbladder, like the coelomic part, lies in a peritoneal cover.

As far as can be determined from gross dissection and microscopic studies of sections through a juvenile fish (*ca.* 5 cms standard length), the tunica externa (*sensu* Fahlén 1967) of the swimbladder is present throughout its precoelomic extension, apparently including the vesicles which lie within the periotic bullae. Further histological study on better preserved material is, however, necessary to confirm these points.

The beginning of the precoelomic peritoneal conduit for the swimbladder is taken

to be the line of demarcation between thick and thin tissue (see above); dorsally, the thick tissue is closely associated with the 6th and 7th vertebrae. As de Beaufort noted, the main part of the conduit is approximately ovoid in form. Anteriorly (below the 1st or second vertebra) it bifurcates to form the "U"-shaped arms associated with the base of the skull, and extending upwards to the openings of the periotic bullae. At the point of bifurcation, the lumen of the ovoid body is deeply constricted, but it immediately expands in the base of the "U"-shaped arms.

Superficially, the egg-shaped body has, in preserved material, a silvery-white colour. Under moderate magnification the tissue appears to be made up principally of horizontally aligned, elongate, parallel and slightly sinuous fibres. Dorsally, this part of the conduit is firmly attached to the ventral and ventrolateral face of the vertebral column. The tissue is thickest along this line of attachment, and it surrounds the basal portion of several ribs which, in consequence, seem to emerge through the wall of the conduit. The point at which the egg-shaped body bifurcates to form the "U"-shaped part is clearly defined externally as well as internally. The "U"-shaped part has very thick walls, and in preserved specimens is yellowish-white in colour. Each arm of the "U" is only half a hollow cylinder but the transversely aligned basal part is a complete cylinder. The arms lie somewhat obliquely forward; the edges of each hemicylinder are closely applied to the skull. Anteriorly and dorso-anteriorly each arm is attached to the intercalar of its side, anteroventrally to the basioccipital, and posteriorly to the exoccipital. The cylindrical transverse part of the "U" is firmly attached to the base of the centrum fused with the basioccipital.

The precoelomic extension of the swimbladder is variously modified. Posteriorly, it differs but little from the region immediately behind the pneumatic duct, and like that region has a non-alveolate inner surface. (For a description of the alveolate main bladder, see de Beaufort, *op. cit.*). Further forward, the cross-section narrows rather rapidly until, at a point about half-way between the anterior bifurcation and the pneumatic duct, the bore is reduced to a narrow duct. As the bore narrows the wall thickens so that over its anterior third the swimbladder has a characteristic appearance, rather like a short section of plastic tubing. Throughout its passage in the peritoneal conduit, the swimbladder is loosely attached to the conduit walls by thin strands of connective tissue.

The thick-walled tube fills the narrow lumen which connects the "U"- and egg-shaped portions of the conduit. It penetrates for a short distance into the base of the "U", and then bifurcates into two, thin-walled tubes, each of which completely fills the space between the skull and peritoneal wall in its arm of the "U". On entering the periotic cavity each tube again expands to form an even thinner-walled vesicle, the periotic vesicle. The outer wall of the periotic vesicle is closely applied to the inner walls of its bony periotic bulla, with diverticula extending into the various recesses of the bulla's inner wall (see below).

Unfortunately, my material is not suitably preserved for detailed histological examination. Thus I cannot determine definitely if both swimbladder tunics contribute to the thick-walled tubular part; nor is it certain whether the periotic vesicle is formed from both tunica interna and externa or from the interna alone.

de Beaufort believed that only the tunica interna lined the periotic region, but then he apparently thought the tunica externa formed the "U"-shaped part of the conduit and therefore remained outside the bulla.

Otic region of the skull. Although the periotic swimbladder vesicles are completely surrounded by bone, they are nevertheless strictly extracranial in position, and lie alongside the lateral skull wall.

Each vesicle lies partly in a horizontally aligned, almond-shaped depression formed in the outer wall of the otic region (*i.e.* in the prootic, basioccipital and exoccipital bones). The greater volume of the chamber is, however, provided by the concave inner face of a shield-like extension from the intercalar. The shield reaches outwards and lateral to the depression in the otic wall, and forms the lateral and ventral walls of the periotic bulla. In other words, this hypertrophied portion of the intercalar forms a false lateral wall to the otic region (see Plate 1, Fig. 1). The space between it and the true lateral skull wall (formed by prootic, basi- and exoccipital bones) being occupied by the swimbladder vesicle. Ridewood's statement (1904, p. 62) that "*Megalops* has a cavity *in* its opisthotic . . ." (*italics mine*) is inaccurate.

There are three, inwardly directed diverticula from the medial (*i.e.* skull) wall of each chamber. From the anterior part there is, ventrally, a broad, deep pit into the floor of the prootic bridge over the myodome. The opening into this diverticulum lies immediately below the anterior tip of the saccular recess in the prootic; the diverticulum of each side is separated in the midline by a thin bony wall. From the posterior part of the chamber there is a dorsomedially directed pit in the exoccipital, and a ventromedially orientated one into the basioccipital. In a dry skull, the ventromedial pits from each side meet one another in the midline of the basioccipital, and are continuous, forming a narrow transverse tunnel underlying the posterior part of the saccular recess. In an alizarin preparation, however, there is a thin bony partition between the medial tips of the diverticula. A foramen (situated immediately below the opening for the hyomandibular branch of the facial nerve) opens into the anterior part of the periotic bulla.

de Beaufort's description of the periotic chamber implies that it is divided into anterior and posterior parts, but none of the specimens that I have examined clearly shows any such division.

The bones forming the inner wall of the chamber (*i.e.* the skull wall) are thick and without foramina or fenestrae. Consequently the periotic swimbladder vesicles are nowhere in direct contact with the sacculus or utriculus (*cf.* the condition in *Clupeomorpha* where there is a direct contact with the utriculus; see Wohlfahrt, 1936).

The myodome in *M. cyprinoides* extends below almost the entire length of the saccular cavity, and the periotic bulla is entirely above and lateral to the myodome.

The intercalar (opisthotic of Ridewood, *op. cit.*) is a large bone of complex shape. For descriptive purposes three parts can be recognized; a relatively small dorso-posteriorly situated basal portion, an expanded lateral shield-like part, and an anterodorsally placed saddle-like wing (see Plate 1, Figs. 2A & B).

The basal part is roughly ovoid in shape, and of rather spongy texture; it has firm sutural unions with the exoccipital medially and the pterotic dorsally.

From the ventrolateral aspect of the basal part there is a short, broad, pedicel connecting it with the expansive, medially concave lateral shield. Posteriorly, the shield is suturally joined with the exoccipital (where it forms the floor to the foramen for the head vein and glossopharyngeal nerve); ventrally there is a suture with the basioccipital, and anteriorly one with the prootic.

The relatively deep dorsoposterior margin of the lateral shield curves medially and somewhat ventrally before expanding to form the broad, saddle-shaped wing. This portion provides the posterior part of the dorsal roof to the periotic bulla. Medially, the hind part of this roofing wing extends upwards and surrounds the basal portion (to which it is very closely applied); it also forms a backwardly directed, almost completely closed groove lying lateral to the basal ovoid (a narrow diverticulum from the periotic vesicle occupies at least part of this groove). The main body of the saddle expands ventrolaterally, and overlaps the upper margin of the lateral shield. In lateral view, the saddle-like wing appears to be an independent crescentic bone closely applied to both the basal part of the intercalar and to its lateral shield-like expansion; the impression is enhanced by the fact that, posteriorly, the crescentic element is suturally joined to a dorsal projection from the shield. However, when the intercalar is isolated from the surrounding skull bones its integrity is at once apparent.

Ridewood (*op. cit.*, fig. 12B, and p. 44) misinterprets certain relationships between the intercalar and its neighbouring bones. He describes the posterosuperior part as "... small and wedged in between the main part of the exoccipital and the part of the bone that forms the posterior border of the subtemporal fossa". The bone which he identifies as part of the exoccipital is, in fact, the posterior, upwardly directed groove formed by the saddle-like wing of the intercalar (*cf.* Plate 2, with Ridewood's fig. 12B).

There are no obvious ontogenetic changes in the morphology of the skull wall in the otic region, such as are seen in *Tarpon atlanticus* (see page 128).

SKULL AND SWIMBLADDER LINKAGE IN *TARPON ATLANTICUS*

In its basic features, the swimbladder-skull connection in this species resembles that of *Megalops cyprinoides*. The chief differences lie in the absence of any contribution from the intercalar to the wall of the periotic chamber (which is formed entirely from the peritoneal tissue), a simpler form of precoelomic peritoneal conduit, and the absence of a thick-walled section in the precoelomic swimbladder extension.

The soft tissues. The precoelomic prolongation of the swimbladder originates immediately anterior to the pneumatic duct. It is of slightly narrower diameter than the main bladder at that point, and is composed of very thin tissue. It almost fills the peritoneal conduit (see below), but, except for a short distance posteriorly in the midline, is free from the conduit walls. The lumen of the swimbladder decreases but slightly as it runs forward. At a point below the first vertebra the bladder divides into two, each arm then passing forward within the periotic chamber. These periotic vesicles are, like those of *Megalops*, very thin-walled; unlike that species there is, in *Tarpon*, no thick-walled tube immediately preceding the point of bifurcation.

The main (*ie.* coelomic) part of the swimbladder, like that of *Megalops cyprinoides*, is alveolate; the description given by de Beaufort (*op. cit.*) for that species could well apply to *Tarpon atlanticus*.

The peritoneal conduit surrounding the precoelomic swimbladder extends from about the 13th vertebra to the 1st vertebra. It is closely applied to the ventrolateral face of the vertebral column and is perforated by the 12th and 13th ribs posteriorly and the first five or six ribs anteriorly. Throughout its length the conduit is of almost uniform diameter, and its walls are of uniform thickness. Unlike *Megalops*, there is no deep ventral groove between the main body of the conduit and the otic arms, which in *Tarpon atlanticus* are just hemicylindrical lateral extensions of the median tube.

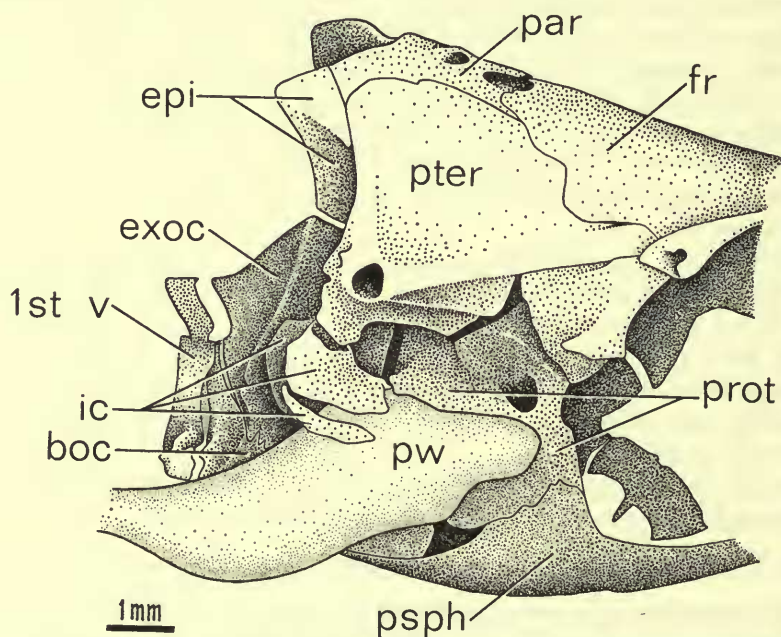


FIG. 1. *Tarpon atlanticus*. Otic region of skull (right) in a specimen 91.0 mm S.L. to show the periotic vesicle (p.w.) Drawn by Sharon Lesure

The otic arms arise at about the level of the first vertebra and run forwards and upwards at a slight angle (see text fig. 1). The ventral and median part of the main tube is, at the point of otic arm divergence, closely applied to the basioccipital.

Each hemicylindrical otic arm extends forward almost to the anterior margin of the prootic. Dorsally it is attached to the lower margin of the exoccipital, to the lower limb of the intercalar (see page 127), along the ventral part of the upper intercalar limb, and along the prootic (following a line level with the intercalar-prootic bridge). Ventrally it is attached to the ascending limb of the parasphenoid (its posterior margin), and to the basioccipital along the parasphenoid-basioccipital suture; the margin of the tube skirts the base of the first infrapharyngobranchial where the latter articulates with the ascending parasphenoid limb.

Otic region of the skull. From the description given above it will be seen that *Tarpon atlanticus*, unlike *Megalops cyprinoides*, has the entire wall of the periotic cavity formed from peritoneal tissue. The intercalar in *Tarpon* serves only as a point of attachment and, to a certain extent, suspension for the peritoneal tissue. In *Megalops* it will be recalled, the peritoneal wall is replaced by a bony plate developed from the lower limb of the intercalar.

The medial wall of the periotic chamber (which is, of course, the lateral skull wall) is formed chiefly by the basioccipital and prootic with a small contribution posteriorly from the exoccipital (Plate 3, Fig. 1). The line of contact between the prootic and basioccipital runs obliquely upwards and backwards; near its antero-dorsal tip, the basioccipital margin diverges slightly from that of the prootic, and a small triangular fenestra is formed. It opens directly into the saccular recess. The fenestra is most obvious in small specimens but it is still present in the largest skull examined (21 cms long). In all specimens throughout the size range available (skull lengths 4.3–21.0 cms) certain areas of the bony inner wall to the periotic cavity are thinner and more flexible than are other areas. The flexible zone is usually centred in the basioccipital, but may include the posterior part of the prootic as well. This condition contrasts markedly with that in *Megalops* where there is neither a fenestra nor thinning of the otic bones. In fact, the otic bones in *Megalops* are noticeably thicker and denser than those of *Tarpon*.

Pronounced ontogenetic changes take place in the morphology of the otic region, particularly with regard to the relative position of the saccular cavity. These changes are discussed below.

The intercalar is a large bone of somewhat complex form (Plate 3, Fig. 2A & B), but relatively simpler than that of *Megalops* (see page 124). Again, three regions can be recognized. The ovoid basal portion fits deeply into the exoccipital; the pit in which it is accommodated lies immediately above the foramen for the vagus nerve. Both the intercalar base and the walls of the pit are deeply ridged, the ridges from the two bones interdigitating.

Two limbs arise from the basal portion. One (the broader and more substantial) is crescentic in lateral outline. Its flattened horizontal portion extends forward to meet the prootic; the vertical portion curves dorsally and articulates with the pterotic. Medially the stout pedicel connecting this limb with the base is firmly articulated with the exoccipital.

The other limb lies below the crescentic one, is less substantial and, apart from its curved posterior margin (which serves as a pedicel) is almost horizontally aligned; it is slightly longer than the crescentic limb (see Plate 3, Fig. 1).

In fishes with a skull length of < 20 mm, the lower arm is well-separated laterally from the upper crescent, but in larger individuals (skull lengths 55 mm and above) the two arms are in contact for most of their lengths (*cf.* text fig. 1, and Plate 3, Fig. 1).

Four levator muscles from the 2nd–4th gill arches originate on the ventral and posterolateral aspects of the lower intercalar limb; the suprpharyngobranchial of the first gill arch articulates near the anterior tip.

Comparing the intercalar of *Tarpon* with that of *Megalops* it is clear that the

expanded, shield-like part in *Megalops* corresponds to the lower limb in *Tarpon*, and that the dorsal, crescentic limb in that species is the homologue of the saddle-shaped wing in *Megalops*. Because the upper crescent in *Tarpon* has a more definite pedicel from the basal part, the base itself has no contact with the pterotic (that contact being effected through the pedicel).

Ontogenetic changes in the shape of the lateral skull wall of the otic region were mentioned earlier. The bones involved are the basioccipital and prootic, especially the former. In all specimens less than 23 cms standard length (skull length 4.3 cms) the wall of the otic region (which is the inner wall of the periotic chamber) is slightly convex, bulging a little into the periotic chamber. The large saccular otolith is visible through the thin bone; its ventral margin lies slightly above the level of the basioccipital-parasphenoid suture.

In two larger skulls (one 13 cms long from a fish 78.2 cms S.L., the other 21 cms long from a fish of unknown length) the lower part of the otic wall (particularly the basioccipital) is deeply concave (see Plate 3, Fig. 1). This once convex area now has the form of an almond-shaped depression. The depressed area lies principally in the basioccipital, below the ventral margin of the sacculus, which now lies in the same horizontal as the lowest point on the ventral intercalar arm. In the 13 cm skull there are two depressions (one in the basioccipital, the other in the prootic) separated by a narrow ridge (see Plate 3, Fig. 1). The posterior, almond-shaped depression in the basioccipital is the larger of the two. In the 21 cm skull, the depressions are confluent.

I have been able to examine only one skull of an intermediate size (5.5 cms, from a fish 31 cms S.L.). Here there is a noticeable concavity in the wall of the basioccipital, posterior and a little ventral to the saccular recess. There is also a shallow indentation of the prootic (just anterior to its suture with the basioccipital) below and in front of the saccular recess. Neither depression is as deep as those in the 13 cm skull, and the lower margin of the sacculus is still ventral in position.

Without more material from the upper part of the "intermediate" size range it is impossible to tell what growth changes are involved in producing the very characteristic form of the otic wall in "large" fishes. The dorsal migration of the saccular recess is particularly intriguing. Measurements made on the otic region in fishes of all available sizes do not indicate a marked differential growth anteroposteriorly or dorsoventrally in any part of the bones involved. There is, however, a suggestion that certain areas in these bones may grow inwards, thereby forming concavities laterally and, as the inner surfaces of the bones extend medially towards one another, the saccular recesses are forced upwards.

THE SACCULAR OTOLITH IN *MEGALOPS* AND *TARPON*

The sagitta in *Megalops cyprinoides* and *Tarpon atlanticus* differs in a number of features (see text fig. 2).

In *M. cyprinoides* the anterior outline is acute, with the ventral margin sloping gently upwards; in *T. atlanticus* it is relatively obtuse, with the ventral margin curved abruptly upwards near the tip. There is a distinct antistrotrum and excisura in *M. cyprinoides* but neither is present in *T. atlanticus*. In that species, the dorsal

outline posterior to the ostium is domed, whereas in *M. cyprinoides* the outline is but slightly curved.

The shape of the sulcus (which is somewhat constricted near its midpoint, has a broad and rounded cauda, and an expansive ostium) is alike in both species.

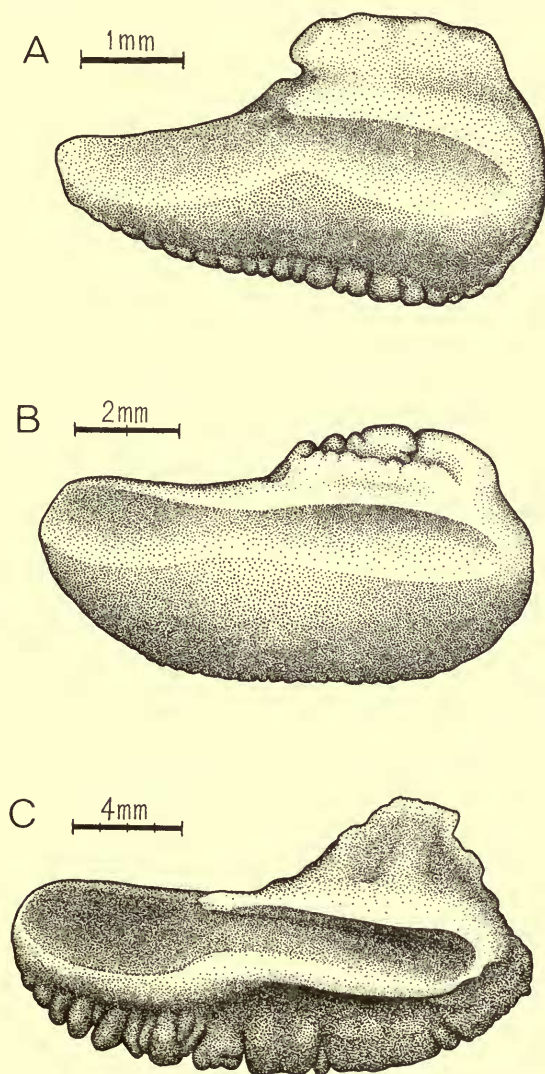


FIG. 2. Saccular otolith (sagitta) of A. *Megalops cyprinoides* (from a fish of unknown length, B. *Tarpon atlanticus* (from a fish 31 cms S.L.). C. *Tarpon atlanticus* (from a large specimen of unknown length).
Drawn by Sharon Lesure

No details of possible growth changes could be determined from the *M. cyprinoides* sagittae available since both pairs are the same size (5.5 mm long). The two pairs of *T. atlanticus* sagittae show that in larger otoliths the dorsal outline is more produced, and the margin of the sulcus is raised and slightly thickened. The smaller sagitta

(10.0 mm long) is from a fish 31.0 cm S.L.; the larger otolith is 21.0 mm long but no record is available of the fish's size.

SWIMBLADDER-SKULL CONNECTIONS IN OTHER ELOPIFORM FISHES

An intimate and complex connection between the otic region and swimbladder exists only in the Megalopidae although in at least some Elopidae a simpler linkage is developed.

Elops lacerta C. and V. (two specimens, 190 and 270 mm S.L. examined) has two narrow, finger-like projections from the anterior part of the swimbladder. These extend forward from about the level of the first vertebra to a point just behind the saccular swelling on the basioccipital. Each projection is closely applied to the basioccipital and lies in a faint groove on that bone. A peritoneal sheath covers each diverticulum, but the tissue is not thicker or in any other way macroscopically distinguishable from the peritoneal layer covering the swimbladder itself.

de Beaufort (1909) describes paired anterior prolongations of the swimbladder in *Elops saurus* Linn., and notes that these reach only as far forward as the middle of the first vertebra. Cuvier and Valenciennes (1846, p. 373) also describe the paired diverticula but do not indicate how far forward they extend (except to note that there is no connection between the swimbladder and the interior of the skull). Finally it may be noted that Hyrtl (1855) makes no mention whatsoever of anterior swimbladder projections in this species.

In contradistinction to these earlier observations I find that the diverticula do extend forward onto the basioccipital (at least in a fish 280 mm S.L.), the situation being identical in all respects with that in *E. lacerta*. These discrepancies are difficult to reconcile; the size of the various fishes examined may, however, be partly responsible (see below).

In *Elops machnata* (Forsk.) (three specimens, two of 175 mm S.L., one 108 mm S.L.) there are two peritoneum covered anterior projections. These extend only to the level of the first vertebra in the larger specimens, and do not even reach that point in the smaller fish. Thus in this species it seems likely that the extent of diverticulum development is positively correlated with the size of the individual.

If in *E. saurus* there is a similar relationship, then the discrepancies between my observations and those of de Beaufort, Hyrtl, Cuvier and Valenciennes might be explained by their having dissected smaller fishes.

No linkage between skull and swimbladder is developed in the two species of Albuloidei I have examined.

In *Albula vulpes* (Linn.) de Beaufort (*op. cit.*) describes a pair of short blind-sacs from the anterior wall of the swimbladder at the level of the fourth vertebra. This is the condition I found in a specimen of 97 mm S.L. (BMNH 1862. 4. 24 : 31) ; the diverticula extend to the level of the anterior rim of the first vertebra. In contrast I could find no trace of diverticula in the other specimens (160 mm and 165 mm S.L. BMNH 1949. 11. 29 : 1 and 1855. 9. 19 : 875) I dissected ; in these fishes the forward end of the swimbladder is smoothly rounded and lies below the first vertebra. Likewise, I find no trace of the anterior diverticula in the swimbladder of *Pterothrissus gissu* Hilgen. (a single specimen 394 mm S.L., the type of *Bathythrissus*

dorsalis Günther). Günther (1887), however, using the same specimen, described two short horns from the anterior wall of the swimbladder, which lies posteriorly in the visceral cavity and thus well behind the strongly developed transverse septum. The viscera of this fish are now in a rather poor state of preservation, and this could well account for my failure to find the horns.

Clearly the situation in elopoid and albuloid fishes requires further investigation on more species and over a wide size-range of individuals. Nevertheless, it does seem certain that no otophysic connection comparable in complexity with that of the Megalopidae, exists in the Elopidae and Albulidae.

DISCUSSION

The status of the genera MEGALOPS and TARPON. There is a great deal of uncertainty about the generic status of the Atlantic Tarpon (see Hildebrand, 1963) ; current opinion seems to favour it being congeneric with the Indo-Pacific species *Megalops cyprinoides*.

Jordan and Evermann (1896) erected the genus *Tarpon* for the Atlantic species, principally on the basis of it having a more posterior insertion of the dorsal fin than *Megalops cyprinoides*. Hollister (1939) showed, however, that the dorsal fin position is the same in both species, but that the ventral fins in *Tarpon* are nearer the snout. In addition she emphasized that *Tarpon* has fewer vertebrae (57, comprising 33 trunk and 24 caudal, compared with 68 [38 trunk and 30 caudal] in *Megalops*), and pointed out differences in the fin ray counts (12-15 dorsal, and 19-22 anal rays in *Tarpon*, cf. 19-21 dorsal and 24-27 anal rays in *Megalops*). Finally, Hollister drew attention to certain differences in the caudal fin skeleton, particularly the longer first uroneural in *Megalops* (see appendix, page 133).

A number of other osteological and soft anatomical differences associated with the swimbladder-skull connection can now be added to those already known. In particular may be noted the entirely peritoneal lateral wall of the periotic cavity in *Tarpon*, the more differentiated precoelomic extension of the swimbladder and its peritoneal sheath in *Megalops*, and the differences in the degree of development and complexity shown by the intercalar in the two species.

At the same time, one should not lose sight of the fact that basic similarity in the "bauplan" of the swimbladder-skull connection seems to stress the phyletic integrity of the two taxa. In this character it seems reasonable to consider the Atlantic species as the plesiomorph partner of the Indo-Pacific species. In other features it is impossible to obtain a clear-cut picture of relative plesiomorphy or apomorphy.

The nature of the interspecific morphological divergence in the swimbladder-skull connection would, nevertheless, seem to warrant the separation of the two species at generic level. Hence I propose to redefine the genera as follows :—

Genus *Megalops* Lacépède 1803 : megalopid fishes with an expanded arm of the intercalar forming the entire lateral wall of the large periotic bulla, which is thus completely bounded by bony walls ; precoelomic extension of the swimbladder with a short, thick-walled section, of narrow bore, immediately posterior to its division into two periotic vesicles ; peritoneal cover to the precoelomic swimbladder

with a "U"-shaped otic portion leading to the periotic bullae anteriorly, and a longer, egg-shaped main body posteriorly; 67 or 68 vertebrae; anterior tip of the first uroneural reaching the anterior part of the second preural centrum.

Genus *Tarpon* Jordan and Everman 1896: megalopid fishes in which the intercalar does not contribute to the lateral wall of the periotic cavity, the latter bounded laterally by precoelomic peritoneal tissue only; precoelomic peritoneal cover of the swimbladder extension passing smoothly into the otic arms forming the lateral walls of the periotic cavity; precoelomic swimbladder extension without a thick-walled tubular portion; 55-57 vertebrae; anterior tip of the first uroneural reaching the anterior part of the first preural centrum.

Relationships between the ELOPOMORPHA and CLUPEOMORPHA. Although Greenwood *et al.* (1966) included the superorders Elopomorpha and Clupeomorpha in a single division (later named the cohort Taeniopaedia, see Greenwood *et al.* 1967) they did so with little conviction, pointing out that if any relationship did exist it was a very distant one. Subsequent research has certainly not provided any new evidence to support any close phyletic grouping of the two taxa. In fact the new evidence indicates quite the contrary situation. For example, a detailed study of the clupeomorph family Denticipitidae (Greenwood, 1968) shows that its supposedly elopomorph-like characters (Greenwood *et al.*, 1966) are not of that nature, but are in fact, clupeomorph characteristics. The earlier confusion was due to insufficient knowledge of denticipitid anatomy. Other research on clupeomorph fishes (mostly unpublished, but see Patterson, 1970) has served to emphasize the uniqueness of this group in a number of specialized characters, characters which in all living and fossil elopomorphs show either no specialization at all or are developed along very different lines.

The swimbladder-otic linkage provides a good example of the latter condition. In the Clupeomorpha the swimbladder diverticula enter the skull, and the vesicles into which they expand are lodged within the bullae developed from the prootic and pterotic bones (or the prootic alone).

In megalopid Elopomorpha (the only members of the superorder with what could reasonably be considered a specialized otophysic connection) the linkage is entirely extracranial and involves different cranial bones. Such a condition could not be considered basic for the otophysic connection characterizing the Clupeomorpha. The otophysic connection found in the Elopidae (see p. 130), on the other hand, is of such a generalized type that it could be basic to either a megalopid or a clupeomorph type. As an indicator of phyletic relationship in this particular context it is valueless. Similar difficulties are encountered when one considers other characters; indeed, the more one analyzes the Clupeomorpha and Elopomorpha, the more difficult it becomes to suggest a close relative for either taxon. In particular, any attempt to find a sister group (*sensu* Hennig, 1966) for the Elopomorpha is hampered by the extreme plesiomorphy of its basal, that is non-anguilliform, members.

Thus, since no positive evidence can be found to support the hypothesis that the Elopomorpha and the Clupeomorpha are each other's closest relatives, I propose that the Clupeomorpha be removed from the cohort Taeniopaedia.

This action, of course, raises the question of where the Clupeomorpha should now be classified. For the moment I can find no satisfactory answer. The clupeomorphs are not the sister group of the other primitive teleost cohort, the Archaeophylaces (osteoglossomorph fishes), and there is, at present, insufficient evidence to include them in the cohort Euteleostei (although this relationship is suggested by some characters). As a temporary expedient, then, the Clupeomorpha will have to be given cohort status and recognized as being a monophyletic group phylogenetically *incertae sedis*. Hopefully they will not remain too long in limbo.

SUMMARY

The skull-swimbladder linkage in *Megalops cyprinoides* and *Tarpon atlanticus* is described and compared. Although both species have the same fundamental bauplan, the linkage in *Megalops* shows greater differentiation of the tissues, in particular the peritoneal cover to the precoelomic swimbladder extension, and the involvement of the intercalar bone in forming a periotic bulla.

In *Tarpon* the peritoneal cover is a simple tube, and the intercalar does not contribute to the formation of a periotic bulla; instead there is a periotic chamber with a non-bony lateral wall (formed from the peritoneal swimbladder sheath). Size correlated changes in the otic region are described for *T. atlanticus*; no such changes occur in *Megalops cyprinoides*.

Other members of the Elopiformes were also investigated, and a simple otophysic connection found in the three *Elops* species examined. *Albula* and *Pterothrissus* lack an otophysic connection.

The disputed generic status of the Atlantic Tarpon (*T. atlanticus*) is reviewed, and it is concluded that this species should be recognized as constituting a monotypic genus, albeit one closely related to *Megalops*. The two genera are redefined.

Finally, the phyletic relationships of the Elopomorpha is considered, particularly with regard to the supposed relationship of these fishes with the Clupeomorpha. There is apparently no positive evidence to support the idea of close affinity, and the Clupeomorpha are given cohort status.

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APPENDIX

NOTES ON THE CAUDAL FIN SKELETON IN *MEGALOPS* AND *TARPON*

I have examined the caudal fin skeleton in three specimens of *Tarpon atlanticus*, and four of *Megalops cyprinoides*. This structure is somewhat more variable in *M. cyprinoides* than was indicated by Hollister (1939). In contrast the characters of

the caudal skeleton that are variable in *M. cyprinoides* are constant in *Tarpon atlanticus*.

Variability in *Megalops* involves the neural arches and spines associated with the first and second preural centra. Two of the four specimens have only a neural arch on the first preural centrum; in the other two specimens this centrum carries a neural arch posteriorly, and an arch with short spine anteriorly. Three specimens (including the second pair noted above) have a neural arch with a fully-developed spine on the second preural centrum; the fourth fish has an arch with very reduced spine, together with an arch and fully-developed spine articulating between this vertebra and the preceding one.

In all three *Tarpon* specimens there is a neural arch (but no spine) on the first preural centrum, and an arch with fully developed spine on the second preural centrum.

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LIST OF ABBREVIATIONS USED IN FIGURES

basph	basisphenoid	ophv	opening for head vein
bic	basal part of intercalar	par	parietal
boc	basioccipital	prot	prootic
boc dep	depression in basioccipital	prot dep	depression in prootic
epi	epiotic	psph	parasphenoid
exoc	exoccipital	pter	pterotic
fica	foramen for internal carotid artery	ptf	posttemporal fossa
fn	foramen for unidentified branch of trigeminal nerve	ptsph	pterosphenoid
fr	frontal	pw	peritoneal wall to periotic chamber
fu V	fused vertebral centrum	soc	supraoccipital
gr	groove	sph	sphenotic
ic	intercalar	stf	subtemporal fossa
ica	saddle-like wing of intercalar	X	foramen for vagus nerve
icagr	posterolateral wall of groove formed by saddle-like wing of intercalar	1st v	first vertebra
icb	lower limb of intercalar	1.	Foramen for head vein
icsh	shield-like expansion of lower intercalar limb	2.	Foramen for hyomandibular branch of VII
icu	upper limb of intercalar	3.	Foramen for orbital artery
io	orbitosphenoid	4.	Foramen
oaf	opening to foramen for orbital artery	5.	Foramen opening into periotic bulla



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PLATE I

FIG. 1. *Megalops cyprinoides*. Otic region of skull in lateral view.

FIG. 2. *Megalops cyprinoides*. Intercalar, A, lateral aspect, viewed somewhat obliquely from above and anteriorly. B, dorsal aspect, the long axis of the bone aligned horizontally.

Drawn by Sharon Lesure

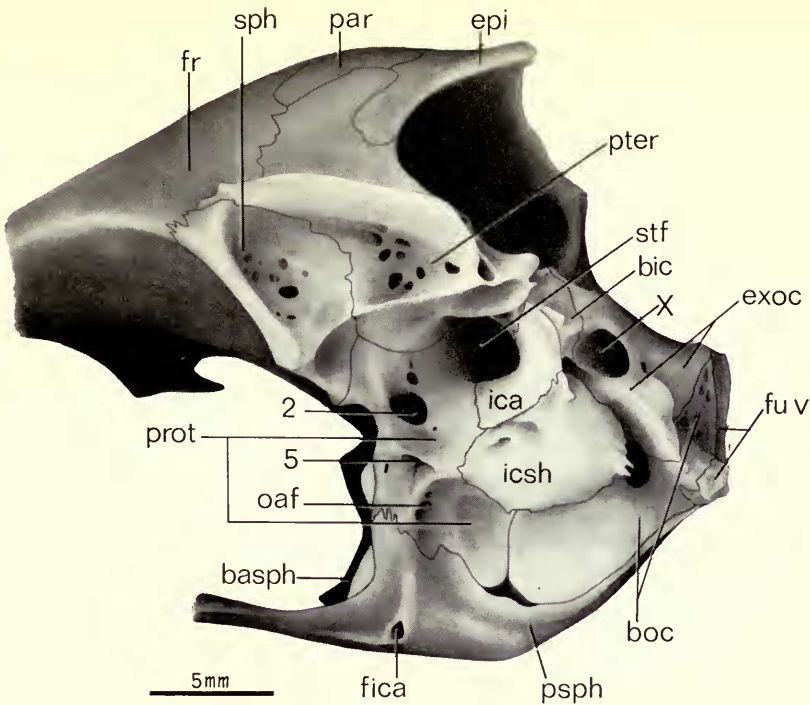


FIG. 1

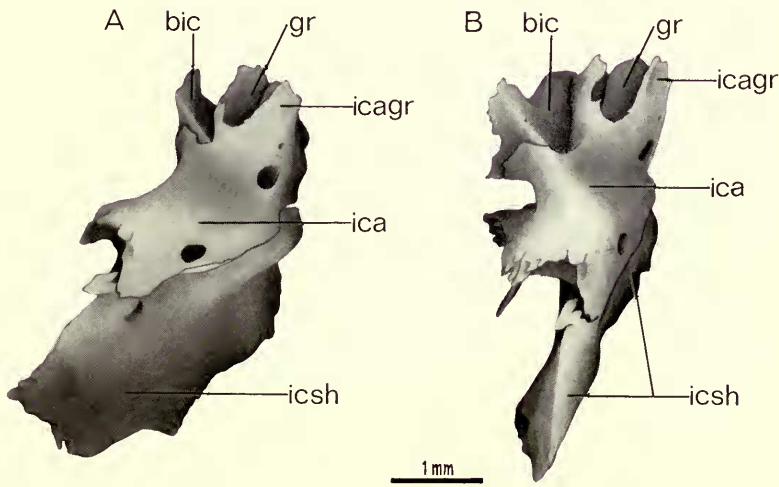


FIG. 2

PLATE 2

Megalops cyprinoides. Posterior aspect of skull, viewed obliquely from the left side and somewhat ventrally.

Drawn by Sharon Lesure

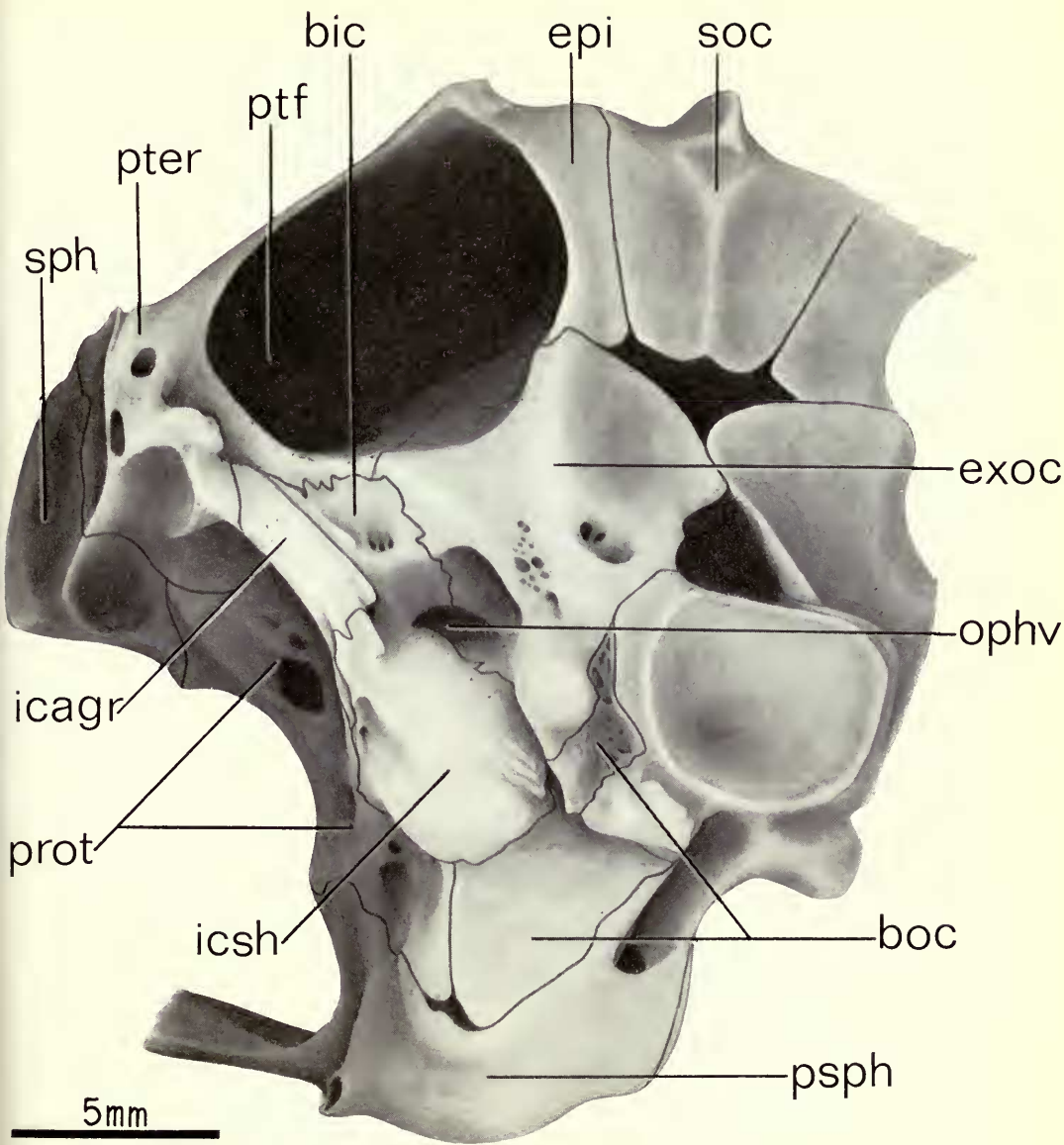


PLATE 3

FIG. 1. *Tarpon atlanticus*. Otic region of skull (from a specimen 78.2 cms S.L.). The foramen numbered 4 is not present in the left prootic, and was absent in other specimens examined.

FIG. 2. *Tarpon atlanticus*. Intercalar and exoccipital. A, Bones orientated in their natural position but viewed obliquely from above and anteriorly. B, Bones orientated in their natural position, but viewed obliquely from above and behind.

Drawn by Sharon Lesure

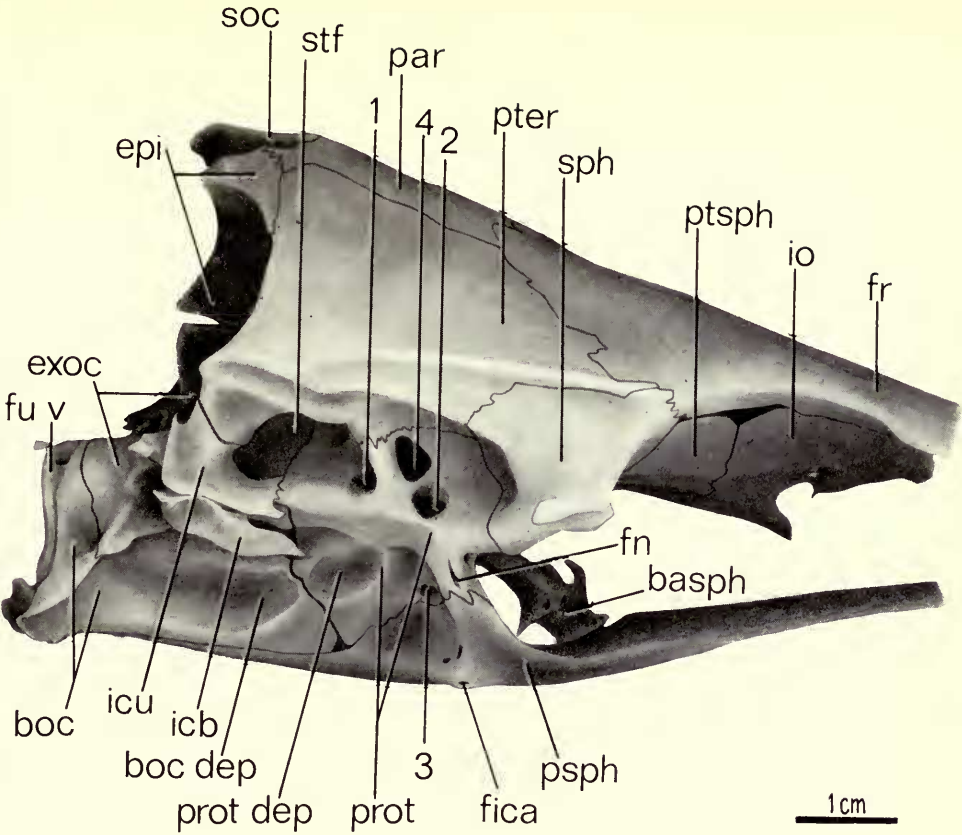


FIG. 1

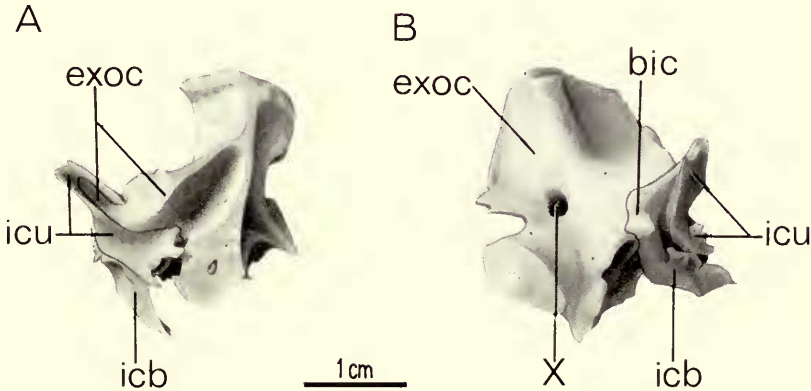


FIG. 2